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SKULL NEMATODES IN MUSTELIDS

By

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The thesis comprises the following papers:

- I. Transmission of the parasitic nematode Skrjabingylus nasicola (Leuckart 1842) to species of Mustela (Mammalia). - Oikos 18:247-252.(1967).
- II Cranial helminth parasites in species of Mustelidae. I. Frequency and damage in fresh mustelids from Sweden. - Oikos 19:217-233.(1968).
- III Cranial helminth parasites in species of Mustelidae. II. Regional frequencies of damage in preserved crania from Denmark, Finland, Sweden, Greenland and the northeast of Canada compared with the helminth invasion in fresh mustelid skulls from Sweden. - Arkiv för Zoologi 22:571-594.(1970).
- IV Seasonal and environmental conditions affecting the invasion of mustelids by larvae of the nematode Skrjabingylus nasicola Leuckart 1842. MS 42 pp.(To be printed in Oikos.)

The papers can be divided into two groups:

II+III Incidence of cranial helminths and skull damage in mustelids

Cranial lesions ascribed to helminths are often reported from mustelids. Five species of nematodes (Skrjabingylus spp.) and one trematode /Troglotrema acutum (Leuckart 1842)/ were known to occur in the nasal sinuses of mustelids.

Fresh material of mustelid skulls from Sweden was studied in order to examine the species and incidence of skull helminths in Swedish mustelids for comparison with preserved skull material in museums in Denmark, Finland and Sweden and with reports from Norway.

The helminths found in the fresh material were S.petrovi Bageanov 1936 in Martes martes (L.) and S.nasicola in all Mustela spp. No trematode was found.

The frequencies of invasion were compared with the intensities of invasion and the frequencies of skull lesions. Regional differences were examined. Skull lesions were found and described in all host species.

Lesions developed rapidly and were most extensive in the smallest mustelids. The frequency and intensity of invasion was greatest in M. putorius L., but the frequency of damage was low. Regional differences were found, the frequency being highest in northern Fennoscandia. Relations were established between rainfall and incidence of parasitism.

I+IV Invasion of *Mustela* spp. by larvae of the nematode *Skrjabinigylus nasicola*

Successful transmission of *S.nasicola* had previously been achieved by feeding mustelids with gastropods experimentally invaded by the nematode. However, species of *Mustela* rarely, or never, feed on gastropods.

Mustelids were fed various animals collected from areas where *S.nasicola* had been frequently found. Only specimens fed on soricids became invaded by *S.nasicola*. Shrews transmitting the parasite were trapped in January through February and October.

By studying the occurrence of young *S.nasicola* females in fresh skull material, recent natural invasions of *Mustela* spp. by *S.nasicola* was established for January, February, March, May, October, November and December. This accorded with the seasonal length distribution of the nematodes.

Certain factors affecting the survival of *S.nasicola* larvae were studied experimentally. The larvae were highly sensitive to desiccation and, when in water, to freezing, but they endured very low temperatures in scats. They left wet scats at all normal field temperatures above zero. The rate of emergence was low at 0°C. The swimming activity dropped by 50 per cent within 3.5 days but larvae lived for about one month in water at +15°C.

The larvae reacted positively to compounds in fresh mucus from *Succinea* spp.

From a study of field temperatures and humidities, it appeared that spring and autumn are the most favourable seasons for larvae survival and transmission. This was at least partly confirmed by the changes in frequency of infestation, which was highest in the cold part of the year.

IV SEASONAL AND ENVIRONMENTAL CONDITIONS AFFECTING THE INVASION OF MUSTELIDS BY LARVAE OF THE NEMATODE Skrjabingylus nasicola

1 INTRODUCTION

Species of Mustela L. are known to be natural final hosts of Skrjabingylus nasicola (Leuckart 1842) Petrov 1927. Invasion and damage by this parasite are frequently reported from mustelids. Transference of the parasite via molluscs to mustelids was successful (Dubnitsky 1956), though mustelids do not normally eat molluscs. Soricids were shown to be naturally invaded by S.nasicola and are possible transmitters of the parasite to mustelids (Hansson 1967).

This paper analyses seasonal variation in invasion and describes environmental parameters affecting the life cycle of S.nasicola. The behaviour and survival of larvae from mustelid scats were examined at known temperatures and humidities. Comparisons are made with the seasonal variations in temperature and humidity experienced in the field in central Scania.

2 MATERIAL AND METHODS

2.1 Laboratory experiments

Two male polecats, invaded by S.nasicola, were trapped in Scania in April 1970. They were kept in cages outdoors at Stensoffa Ecological Station and their scats were used for laboratory experiments on the larvae of S.nasicola. The cages, placed in shade, were covered to raise the humidity and to protect the scats from drying wind. Scats produced during the night (8 PM - 8 AM) or within 2 hours during day-time were used as "fresh scats". The scats were collected on a piece of wall board just under the net bottom of the cages. The scats were put into plastic bags and immediately taken to the laboratory for experiments. At the time of use the scats were often broken into pieces.

Most scats used in studies of larval emigration were baermannized in test-tubes for 28 hours at +20°C or 48 hours at +15°C to obtain the total number of emerging larvae. Then the scats were dried at +105°C and weighed to determine the number of larvae per g dried scat.

Larvae baermannized in tap water were used for experiments on the behaviour of larvae in water. In defining the activity of mobile larvae, undulating movements are regarded as swimming. Less active larvae are those which irregularly, or occasionally, move head or tail.

A dissecting microscope (40 x enlargement), usually provided with a heat protecting filter, was used for observation of the larvae.

2.2 Field studies

Field data on temperature and relative air humidity (RH) were collected by thermograph and hygrograph at two places near Stensoffa Ecological Station in central Scania, where minks regularly deposit infested scats. One was a log in a brush wood (birch) in a swamp, the other an exposed wooden bridge in an open meadow. Mean values were calculated from the data of every second hour. The extremes of each 24-hour cycle were used for computing seasonal maximum and minimum values.

The months were grouped as follows. Spring: March-May (88 24-hour measurements). Summer: June-August (81). Autumn: September-November (115). Winter: December-February (71).

2.3 Studies on fresh skull material

Seasonal variation in final host invasion was studied using fresh skulls of Mustela spp. obtained in Sweden (Hansson 1968). The material consisted of 55 Mustela nivalis L. (138 nematodes), 172 M.erminea L.(872), 35 M.putorius L.(509) and 126 M.vison Schreber (128).

The length of the nematodes was measured using fresh or, more usually, frozen material. Small nematode females lacking free larvae in the uteri, though accompanied by male(s), were considered to have invaded their mustelid host less than four weeks before trapping. Larvae have been found in scats of M.nivalis and M.putorius 18-25 days after invasion by S.nasicola (Dubnitsky 1956, Hansson 1967).

The mustelid skulls were grouped by age on the basis of the coalescence of the external sutures of ossa nasalia (Hansson 1968). The age groups for different species may not be exactly equivalent.

The geographical grouping into four regions is the same as in Hansson (1970). Regions I + II represent roughly the southern half of Sweden, regions III + IV the northern half.

3 LABORATORY EXPERIMENTS

3.1 Emergence of larvae from wet scats

It is known that the larvae leave the scats under wet conditions. To examine the rate of larval emergence from wet scats, the number of free larvae were counted at intervals until emergence ceased. For this purpose fresh scats containing larvae were put on slides (one scat per slide) at room temperature ($+22^{\circ}\text{C}$). Tap water at room temperature was added until the scats were covered by a water film. At intervals the scats were rinsed and then moved to other slides, where new water was added. Ninety per cent of the larvae left the scats within 4 hours and 99 per cent within 24 hours (Fig 1).

Baermannization at $+16-18^{\circ}\text{C}$ for 9 hours caused the emergence of 91.9 per cent (three series, 0.38 g, 1670 larvae) of the larvae; after 12 hours 99.2 per cent (three series, 0.19 g, 1248 larvae) had left the scats.

In nature the temperature of water varies greatly, from zero upwards, during the year (see Sect. 4). Therefore the rate of emergence at different temperatures was measured. The temperatures chosen were $\pm 0^{\circ}$, $+4^{\circ}$, $+15^{\circ}$ and $+26^{\circ}\text{C}$. The material used was as follows: at 0°C , seven series, 2.87 g, 3766 larvae; at $+4^{\circ}\text{C}$ four series, 0.56 g, 1133 larvae; at $+15^{\circ}\text{C}$ four series, 0.70 g, 1869 larvae; at $+26^{\circ}\text{C}$ five series, 0.81 g, 6679 larvae. In the series run at 0°C scats were put into petri dishes and placed in a covered plastic box filled with ice and water; after 30-60 minutes water at 0°C was added. In four series the dishes containing free larvae were changed at 40 minutes intervals, and in the other three series, at intervals of 20 minutes. The temperature variation was $0^{\circ} - +0.5^{\circ}\text{C}$. At test temperatures above 0°C , slides were used instead of petri dishes for the extraction of larvae.

After 360-480 minutes the larvae remaining in the scats were baermannized at room temperature (see Sect. 2.1 and Fig 1), preserved in formalin-alcohol and later counted. The activity of the larvae increased with increasing temperature (Fig 2) although

initially the emergence rates were similar. The relation between the percentage of the larvae emerged (y) at all temperatures and the time (X) was found to fit significantly the regression equation $y = k \log (x + 1)$ (At 0°C : $r = +0.60$, $t = 7.58$, $P < 0.001$; at $+4^{\circ}\text{C}$: $r = +0.92$, $t = 20.19$, $P < 0.001$; at $+15^{\circ}\text{C}$: $r = +0.95$, $t = 25.16$, $P < 0.001$; at $+26^{\circ}\text{C}$: $r = +0.94$, $t = 19.08$, $P < 0.001$). The differences in the slopes of the various regression lines were tested and the emergence rate was significantly slower at 0°C ($b = 14.84$) than at $+4^{\circ}\text{C}$ ($b = 26.42$, $t = 3.53$, $P < 0.001$), at $+15^{\circ}\text{C}$ ($b = 33.64$, $t = 4.76$, $P < 0.001$) and at $+26^{\circ}\text{C}$ ($b = 34.30$, $t = 4.75$, $P < 0.001$). The slope of the regression line at $+4^{\circ}\text{C}$ was significantly lower than at $+26^{\circ}\text{C}$ ($t = 2.29$, $P < 0.05$) and at $+15^{\circ}\text{C}$ ($t = 2.22$, $P < 0.05$).

Comparison of the contents of dishes changed at 20 minutes intervals with those changed at 40 minutes intervals showed no difference, i.e. the number of changes did not influence the emergence rate.

The number of larvae per g dried scat varied considerably not only between scats but even within the same scat when baermannized within 5 minutes after deposition (e.g., within one scat: 1383 - 6820 larvae/g). Most larvae were found in the proximal part of two scats investigated in more detail. When the densities of larvae from dried scats of the same origin were compared the differences were found to be unrelated to the size of the scats or samples (proportionally 18 + and 21 - in 39 comparisons of larger and smaller parts). Thus the number of larvae surviving in dried scat could not be used for measuring parameters such as survival rate, because of the great and irregular individual variations.

3.2 Emergence of larvae from scats kept at high relative humidity

Petri dishes (50-mm diameter) containing tap water were placed in circular, covered plastic chambers and surrounded with distilled water or a saturated salt solution (Winston and Bates 1960). A plastic dish (25 mm in diameter, 6 mm high) holding wooden sticks was placed in each petri dish and scats containing larvae were placed on the sticks. At intervals (up to 11 days at $+15^{\circ}\text{C}$) each chamber was checked and the larvae located: the scats were placed on slides and water was added 60 minutes before checking for larvae. Both plastic and petri dishes were also checked for larvae.

In all cases (20) there were great numbers of living larvae in the scats. A few larvae (one to four, in one case 11) were found in less than 50 % of the plastic dishes. There was no clear difference in larval behaviour between the two relative humidities (100 % and 97 %) and temperatures (+15°C and +26°C) studied. There were no larvae in the petri dishes. Thus larvae do not normally leave scats at high relative humidity. The few larvae found in the plastic dishes may have emigrated in condensed water.

3.3 Influence of humidity and temperature on activity and longevity of larvae

3.3.1 Larvae in the scats

Fresh scats containing larvae were placed on a net above P_2O_5 (0% RH) and saturated salt solutions in circular covered plastic chambers. The salt solutions used were: $Mg\ Cl_2 \cdot 6\ H_2O$ (32.5 - 34 % RH), $CaCl_2 \cdot 6H_2O$ (40 % RH at +4°C), $K_2CO_3 \cdot 2\ H_2O$ (43-47 % RH), $Ca(NO_3)_2 \cdot 4\ H_2O$ (50 % RH), NaCl (75 % RH), K_2SO_4 (97.5-99 % RH), aqua dest. (100 % RH) (Winston and Bates 1960). The investigations were carried out at +4°, +15° and +26°C. The scats were analysed at intervals for living larvae to determine the duration of larval survival. The scat was put on a slide at room temperature and water was added. After 30 minutes presence or absence of swimming larvae was recorded.

The maximum number of days for which scats could be left at a certain temperature and relative air humidity and still produce active larvae is shown in Fig 3. The temperature greatly influenced the longevity of the larvae at the various humidities, the time during which activation was feasible being considerably shorter at higher temperatures. Larvae were emerging from scats kept at 100 % RH until the 66th day at +4°C while at +26°C no larvae emerged after the 8th day. Less active larvae emerged from scats kept for a somewhat longer time at each relative humidity.

A determination of the active larvae leaving the samples and the larvae remaining there at successive examinations was impossible but some indication of the changes was obtained by a further examination of the two series kept at 34 % and 76 % and +15°C, using two other methods.

I Interval tests were made as in Sect. 3.1, at +26°C, in petri dishes; dishes containing emerged larvae were changes at 40-minute

intervals up to 360 minutes and the last emerging larvae were obtained by baermannization for another 24 hours. No clear picture of the emergence rates was found but the rate of emergence seemed to be slower the longer the scats were kept at the various humidities. A few less active larvae emerged from scats kept at 34 % RH for 3.5 days.

II Some of the scats kept at 34 and 76 % RH were baermannized at $+15-16^{\circ}\text{C}$ for four hours. Then the test tubes containing emerged larvae were changed. The baermannization was then continued for 24 hours at the same temperature and the larvae were counted. The proportion of the total number of emerged larvae that emerged within four hours seemed to drop more slowly from scats kept at 76 % RH (after 3.5 days: mean 78 per cent, Σ 693 larvae) than from scats kept at 34 % RH (after 1.5 days: mean 82 %, Σ 801 larvae). The corresponding values for a fresh control were: mean 93 %, 2930 larvae. The length of time for which scats could be left at 76 % RH and 34 % RH and still contain larvae, which were activated by 4 hours in water, agreed with the results obtained by exposing the scats to water on a slide for 30 minutes.

3.3.2 Desiccation of emerged larvae

Larvae from one fresh scat, baermannized for one hour at $+22^{\circ}\text{C}$ and then stored at $+17^{\circ}\text{C}$ for 5 hours, were used. Drops of water containing swimming larvae were placed in a petri dish at $+24^{\circ}\text{C}$ and 40 % RH. A pipette and a filter paper were used to remove water from a group of larvae. The time of desiccation was measured from the moment when the movements of the larvae stopped because they were dry, until water was added for examination of larvae. The error in time estimate may be ± 5 seconds. After adding water, the numbers of swimming and less active larvae were counted. Intact drops of water containing swimming larvae were used as controls. After 70 minutes the swimming activity of the control larvae was only 6.7 per cent less than at the start.

Of larvae desiccated for 2 minutes, 51 per cent regained swimming activity and another 15 per cent moved irregularly (Fig 4). None of those desiccated for 3 minutes started to swim, and only 6.5 per cent showed any movement; no larva desiccated for 5 minutes was revived. Evidently the larvae are strongly affected by desiccation even for a short period.

3.4 Longevity of larvae in water

Larvae baermannized in tap water were placed in petri dishes, 50 mm in diameter. Boiled tap water was added. The water was aerated with 40-60 bubbles per minute and the dishes kept at $+15^{\circ}\text{C}$. They were examined at regular intervals for active larvae. Some dishes were shaken vigorously about 20 times and then allowed to settle before the larvae were counted. The proportions of swimming and less active larvae were calculated from the number of swimming and less active larvae present at the start.

A sample of 91 active larvae showed a rapid drop in activity when undisturbed. Agitation increased the activity strikingly during the first days, but thereafter had a small effect (after 5 days: 30 per cent of the larvae swimming before, and 97 per cent after agitation; after 8-13 days: 9-12 per cent before and 34-45 per cent after agitation; after 16-20 days: 2-3 per cent before and 8-11 per cent after agitation).

The decrease in activity of four series of not agitated larvae was examined in more detail (Fig 5). In order to calculate the time taken for the number of swimming larvae to decrease by 50 per cent, the figures used in Fig 5 were assumed to fit the formula $N_t = N_0 \cdot e^{-rt}$ where N_0 = the number of swimming larvae at the start, N_t = the number of swimming larvae after t days, e the base of the natural logarithms and r the rate of disappearance. However, as no swimming larvae were found at the end the formula was changed to $^e\log (N_t/N_0 + 0.01) = -rt$. The formula denotes a "mortality" with a constant proportion of animals disappearing per time unit. The assumption was tested, and the points fitted the curve significantly ($r = -0.83$, $t = 11.53$, $P < 0.001$).

The regression equation computed ($^e\log (N_t/N_0 + 0.01) = -0.21 t$) showed that 50 per cent of the animals stopped swimming within 3.5 days. After one to two weeks less than 10 per cent were seen swimming and about one month after the emigration from the scats the last larvae stopped swimming; less active larvae were found for the last time on the 24th, 28th, 29th and 33rd day after emigration in different series of observations.

3.5 Effects of freezing on survival and activity of larvae

One freshly killed ermine was kept at -20°C for 10 days, and then

examined for parasites after 7 hours at room temperature. Dead adult female S.nasicola dissected from the skull, contained vigorously swimming larvae.

Fresh scats containing larvae were put into plastic bags and kept at -20°C . At intervals scats were analysed for living larvae; they were thawed at $+4^{\circ}\text{C}$ and put on slides with water. Swimming larvae were found in the water from scats kept at -20°C for 77 days. Larvae frozen in water at -20°C did not survive.

Some tests were carried out at temperatures more usual in the field. Fresh scats were kept in open petri dishes at -5°C for five days and then analysed for living larvae, after acclimation at $+4^{\circ}\text{C}$ (14 hours) and $+15^{\circ}\text{C}$ (one hour). The rate of larval emigration was determined by covering the scats with water at $+15^{\circ}\text{C}$ and changing the water at 40 minutes intervals. The number and activity of larvae removed after each interval was recorded (Fig 6:2).

The alternation of freezing and thawing in nature was simulated by exposing scats in petri dishes to alternations between -5°C and $+4^{\circ}\text{C}$ at 24-hour intervals. When the scats had been frozen and thawed four times they were examined as above for living larvae and their emigration rate (see Fig 6:3).

Living larvae appeared from every scat frozen without water. Each of the three curves in Fig 6, showing rates of emergence from scats kept under various conditions, fits the equation $y = k \log (x + 1)$ (curve 1-fresh scats: $r = +0.95$, $t = 16.66$, $P < 0.001$; curve 2: $r = +0.79$, $t = 9.47$, $P < 0.001$ and curve 3: $r = +0.92$, $t = 13.69$, $P < 0.001$). The differences in the slopes of the three curves were tested by pairs. Curves 1 ($b = 34.29$) and 2 ($b = 20.51$) demonstrate significantly different emergence rates ($t = 3.16$, $P < 0.001$). Curves 2 and 3 ($b = 25.63$) were not significantly different.

The numbers of larvae removed after up to 320 minutes in water were combined for examination of the mobility of the larvae. Out of the 1378 larvae collected from scats (1.06 g) kept at -5°C for five successive days, 30 per cent were active, compared with only 6 per cent of the 768 larvae collected from scats (0.67 g) alternated between -5°C and $+4^{\circ}\text{C}$. The difference is highly significant ($\chi^2 = 167.17$, $P < 0.001$).

Finally larvae baermannized in tap water were tested at -5°C . 387 larvae (96 per cent swimming, one per cent less active) were kept in water in petri dishes at -5°C for five days after acclimation to $+4^{\circ}\text{C}$. Sixteen hours after thawing at $+4^{\circ}\text{C}$ all were immobile. Of 46 larvae in water frozen at -5°C for 9 hours, three were swimming and ten were less active, 100 minutes after thawing at $+19^{\circ}\text{C}$. Thirtyfive minutes later, no larvae were swimming and only three were less active. Out of 267 larvae cooled but removed to $+19^{\circ}\text{C}$ just before freezing, the percentage of swimming larvae was about the same after as before cooling: 94 per cent before and 90 per cent after. Thus the freezing of wet larvae is fatal.

3.6 Response of larvae to *Succinea* mucus

In water the swimming of invasive larvae was ineffective and undirected. When, however, the larvae were offered soaked gelatine (at 100% RH and $+21^{\circ}\text{C}$), they moved at a mean velocity of ca 0.05 mm/sec. There was no clear photopositive or photonegative reaction to weak day light. But when mucus from the snail *Succinea* sp. was added to the water, nearby larvae started to move vigorously towards it. They were extremely active, and bored into the mucus with jerking spiral movements of the front end. Within 10-15 minutes numerous larvae surrounded the slime; these larvae were much more active than those in the open water.

4 FIELD STUDIES

If temperature and humidity conditions experienced by *S.nasicola* larvae in mink scats in central Scania (Figs 7 and 8) are compared with the survival of larvae at constant temperatures and humidities in the laboratory (Sect. 3.3.1 and Fig 3), it is found that in all seasons, at both sheltered and exposed sites, the larvae may survive for a week or more. However, periods of extreme values - maximum temperature and minimum humidity - may kill the larvae.

Temperature and relative humidity were recorded continuously and means calculated for every second hour. The values at all seasons in brushwood would allow a survival of more than one week (Fig 7). The spring average (I) would permit about 12 days survival and the summer average (II) about one week, while periods of adverse extreme conditions correspond to a survival of about one and a half day in spring and one day in summer. Such extreme periods, however, usually last only one hour and always less than a day.

In autumn (III) and winter (IV) larvae may live for one week or more. The average autumn conditions permit about three weeks' survival. Conditions for survival are most favourable in winter.

In all open field, diel variations in temperature and humidity are great, especially in summer. The mean maximum temperature and mean minimum humidity in winter would allow survival for about two weeks, but the average temperature is below freezing which is usually fatal (Sect. 3.5). In spring and autumn, the overall means correspond to an experimental longevity of about 12 days. In the driest and warmest periods, the larvae could only live for three days. A lifespan of three days is possible also under average summer conditions, but at adverse conditions the larvae will die within one day.

5 SEASONAL VARIATION IN THE NATURAL INVASION OF Mustela spp. BY S. nasicola

5.1 Fresh invasions

Mustelids trapped in January, February, March, May, October, November and December had been invaded by S.nasicola for less than four weeks (Tab 1). Out of twelve Mustela, three were probably invaded for the first time. These were one M.nivalis of age group 2, one M. vison of age group 2 and one M.erminea of age group 3. The female nematodes in these hosts were young, containing no or single larvae, while fertile adult females were crowded by larvae (Tab 1). The remaining specimens (M.erminea, and M.putorius of age groups 3 and 4) had had previous invasions.

Seasonal variations in frequencies of recently infested mustelids and of their S.nasicola females were analysed. Ten per cent of 120 mustelids had been invaded recently; they contained 738 S.nasicola, three per cent denoted young. No fresh invasions were found in summer, but few skulls were available for examination. No significant seasonal differences were obtained; the values for autumn, winter and spring were similar, but frequencies were low.

5.2 Seasonal frequencies and intensities of invasion

Examination of the entire collection of Mustela skulls showed no seasonal difference in frequency of invasion. This is partly because there was insufficient material for some times of year, and partly because there are regional differences in invasion, and

sex differences in frequency of invasion in M.erminea (Hansson 1970). When the material was divided into two groups, viz June-November (summer+autumn) and December-May (winter+spring), there were still no clear differences. A comparison of the material from December-January with that from February-May showed a higher frequency in December-January in M.erminea from regions III+IV (both sexes) and M.vison from regions I+III+IV. This difference was significant in males of M.erminea, and in M.vison:

	December-January		February-May		χ^2	P
	Σ	% invaded	Σ	% invaded		
<u>M.erminea</u> (males)	28	82	26	58	3.87	<0.05
<u>M.vison</u>	34	68	34	38	5.90	<0.05

In M.erminea from the northern part of Sweden (region III+IV in Hansson 1970) the mean number of S.nasicola per invaded host increased from summer (2.5, 2 hosts) and autumn (6.9, 13 hosts) to winter (11.1, 43 hosts) and spring (12.6, 16 hosts). The highest mean number was found in February (18.2, 14 hosts). In June-November the mean number was 6.3 and in December-May 11.3. The mean number ($\bar{X} \pm SE$) in autumn (6.9 ± 2.1) as well as in December (7.0 ± 1.5) was significantly lower than the mean number in January-May (13.3 ± 2.0) ($t = 2.24$, $P < 0.05$ and $t = 2.52$, $P < 0.05$ respectively). The mean numbers of nematodes in M.erminea in December-January (7.4 ± 1.3) and in February-May (15.6 ± 2.6) were significantly different ($t = 2.20$, $P < 0.05$). In M.nivalis there were similar differences in mean numbers: 3.6 in June-November (43 hosts), 4.3 in December-January (43 hosts) and 8.3 in February-May (50 hosts). In M.vison and M.putorius no seasonal variations in mean number of nematodes per infested individual were found.

5.3 Body length distribution in S.nasicola

Host species with a great abundance of parasites viz. M.erminea and M.putorius were examined more closely. The S.nasicola material from M.erminea trapped in the northern part of Sweden (region III+IV in Hansson 1970) showed seasonal variation (Fig 9). In spring the frequency distribution by length of both male and female S.nasicola was binodal, the distribution by length of males being significantly different from a normal distribution: $\chi^2 = 6.37$, $df = 2$, $P < 0.05$. The corresponding female distribution in spring

gave $\chi^2 = 5.13$, $df = 3$, $0.20 > P > 0.10$. The mean lengths of both sexes were highest in autumn. In females the mean length in autumn (18.7 ± 0.8 mm) was significantly greater than in winter (16.9 ± 0.3) ($t = 2.11$, $P < 0.05$). The corresponding values for female length in spring (17.0 ± 0.5 mm) compared with the length in autumn were: $t = 1.80$, $0.10 > P > 0.05$. The mean lengths of males were similar in winter, spring and autumn (9.1, 9.0 and 9.4 mm respectively).

The S.nasicola material from M.putorius (southern Sweden) showed similar seasonal variations in length distribution and mean body length (Fig 10). In spring the frequency distribution by length of both males and females was binodal differing significantly from a normal distribution: males $\chi^2 = 10.41$, $df = 3$, $P < 0.05$; females $\chi^2 = 6.79$, $df = 2$, $P < 0.05$. In winter and autumn there was no significant difference from normal distribution. The mean lengths of both sexes were highest in autumn. The mean length of males in autumn (10.7 ± 0.3 mm) was significantly higher than in winter (9.8 ± 0.3 mm) ($t = 2.12$, $P < 0.05$). The mean length of females in autumn (22.7 ± 0.7 mm) was significantly higher than in winter (20.5 ± 0.7 mm) ($t = 2.22$, $P < 0.05$) and spring (20.3 ± 0.5) ($t = 2.79$, $P < 0.01$).

6 DISCUSSION

The emergence rates from fresh scats appeared independent of scat weight and of the extraction methods used (see Sect.3.1). Neither was there any evidence of a diel variation in the abundance of larvae obtained. The consistency of the scats may therefore be the main quality influencing the emergence rate. The lower the activity of the larvae, the more important the consistency of the scats. This may cause the greater variations in emergence at lower temperatures, especially at $\pm 0^\circ\text{C}$ (see Fig 2).

The great variation in larvae/g dried scat may be explained by an active migration of the larvae within the intestines of the host, as has been reported in related nematode larvae. The larvae accumulate in the posterior parts of the intestine, especially the coecum. Such larvae are often attached to the surface of the scats, (Hobmaier 1934). The emergence of S.nasicola larvae from wet scats, whatever the temperature, may indicate that they are on the surface. Under such circumstances low activity may be sufficient for release.

The estimated survival time (Fig 3) certainly does not represent maximum time of survival, because only limited amounts of material were investigated and scats were only soaked for a short time. However, the values presented accorded with changes in larval activity. Evidently, the longevity of S.nasicola larvae is not very great compared to that of other nematode larvae (Kates 1965). First stage larvae of Muellerius capillaris (Mueller 1889) from vertebrate herbivores (sheep, goat) were able to live for at least 40 weeks outdoors during winter in England (Rose 1957), and Kates (1965) reported survival for several months of larvae immobilized at low temperatures above 0°C. The longevity of Anafilaroides rostratus Gerichter 1949 - a parasite of cats, belonging to the same family as Skrjabinylus - is similar to that of S.nasicola (Seneviratna 1959).

The swimming activity of S.nasicola larvae decreased rapidly: in 3.5 days at +15°C it had decreased by 50 per cent and agitation restored the activity for only a very short time (Sect.3.4). According to Dinnik (1980) Skrjabinylus larvae have small energy reserves which will explain the limited survival, especially at +26°C when the metabolism is high (see Fig 3).

Temperature ranges and temperature optimum of terrestrial nematode larvae may vary with the geographical region (Bird and Wallace 1966 etc) but the optimum is normally between 20 and 30°C (Kates 1965). The optimum temperature for rapid emergence of S.nasicola larvae from wet scats seems to be between 20 and 30°C (see Fig 2). The lower the temperature, the lower the activity, but even at zero S.nasicola larvae leave wet scats. In Canada Anderson (1962) found some activity of larvae of the lung nematodes Aelurostrongylus pridhami Anderson 1962 and Filaroides martis (Werner 1922) from mink just above freezing, but activity rose considerably with increasing temperature.

All larvae of M.capillaris survived 24 hours at +8°C after having been frozen in water at -2 to -7°C for up to three days, and some specimens survived freezing for more than a week (Rose 1957). Larvae of A.pridhami and F.martis may also survive freezing for a few days (Anderson 1962). However, the activity and longevity of the thawed larvae were affected.

S.nasicola larvae, however, are not well adapted to temperatures below zero: 1) freezing in water is fatal, 2) repeated freezing

and thawing of scats affect movements of contained larvae strikingly and 3) freezing for one week affects the larval emergence rate (Sect. 3.5). Seneviratna (1959) reported that A.rostratus was killed by freezing overnight, but this relative of S.nasicola is found in warm regions (Palestine, Ceylon).

Some nematode larvae have considerable ability to survive desiccation. A number of authors (Rose 1957, Anderson 1962 etc.) have reported that M.capillaris survives for considerable periods in dry environments. However, the sensitivity of S.nasicola larvae to desiccation is very high (Sect. 3.3.2) and similar to that of A.pridhami and F.martis at similar temperature and humidity conditions (Anderson 1962). A.rostratus larvae died after desiccation for five minutes (Seneviratna 1959).

The assumption that chemosensitivity enables nematodes parasiting snails to find host animals is supported by observations that larvae react to mucus (Sect.3.6), and penetrate the snail foot at the site of mucus glands (Hobmaier 1934, Dubnitsky 1956). S.shitwoodorum Hill 1939 may also be ingested with the food (Hobmaier 1941) as is the case with A.pridhami and F.martis (Anderson 1962).

In spite of ineffective movements when suspended in water, stated also for related nematodes (Morgan 1929, Hobmaier 1934, Anderson 1962), the larvae of S.nasicola move around on certain moist surfaces (Sect.3.6). Their reaction to the presence of fresh snail mucus from Succinea (Sect. 3.6) indicates a positive chemo-kinesis towards mollusc hosts (see Croll 1970).

Examination of skull material from Sweden showed that the invasion of Mustela spp. by S.nasicola takes place during the cold part of the year. Invasion of both M.erminea and M.putorius starts late in the autumn, since 1) mean lengths of winter specimens were less than those of autumn specimens (Figs 9 and 10), 2) recently infested hosts were found in December, and 3) the frequency of invasion in M.erminea is high in December-January. The frequency distribution by length of S.nasicola in spring indicated the presence of two overlapping nematode generations (Figs 9,10). The high mean number of S.nasicola in M.erminea trapped in February-May and the number of fresh invasions in both M.erminea and M.putorius at this period showed that invasion continues during winter and spring. The high mean length of nematodes from

M.erminea and M.putorius in autumn may indicate that these specimens of S.nasicola had mainly entered the hosts the previous spring.

The great seasonal variations in infestation of M.erminea may indicate a higher mortality of infested individuals. Thus the frequency of invasion is significantly lower in February-May than in December-January, although the mean number of nematodes per infested individual is significantly higher in February-May. These variations also suggest that the lifespan of M.erminea is usually about one year, as is reported by Fog (1969) who trapped no old animals in late summer or autumn. Van Soest and van Bree (1970) also found a rapid turnover in ermine populations.

S.nasicola produced larvae continuously for at least three years in captive M.nivalis (Hansson 1968), so the parasite probably survives for the lifetime of M.nivalis and M.erminea.

The transmitters of S.nasicola to mustelids have been reported as molluscs (Petrov and Gagarin 1937, Petrov 1941, Popov 1943, Ericson 1946, Vik 1955, Dubnitsky 1956, Shimalov 1963) and frogs (Wegelin 1930, Baer 1931). But, as the invasions in Mustela spp. probably occurs in winter, molluscs or frogs hardly transmit the parasite. Lankester and Anderson (1966) found larvae of F.martis and A.pridhami in the liver of wild soricids, but no Skrjabinylus larvae. Lankester (pers.comm.) later found that Skrjabinylus larvae enter the body musculature and not the liver, which is the usual site of lung nematode larvae. This supports the observation of Hansson (1967) that soricids are vectors.

Gastropods have been experimentally invaded by S.nasicola (Dubnitsky 1956); they are regularly eaten by Sorex araneus (L.) (Mezhzherin 1958) and may serve as the first vector of S.nasicola. Invasion of molluscs by larvae of lung nematodes occurs even at low temperatures (Anderson 1962).

The first intermediate host is probably invaded in autumn and spring when temperature and humidity are periodically favourable; summer seems to be the most adverse season for nematode larvae in exposed mustelid scats.

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ABSTRACT

Larvae emerged from wet scats at all field temperatures above zero. Emergence was significantly slower at 0°C. Larvae survived in water for one month at +15°C but swimming activity declined by 50 per cent within 3.5 days. For a very short time swimming activity could be restored by agitation. Low humidities and high temperatures reduced survival within scats.

Larvae desiccated for 5 minutes were killed. When frozen wet, no larvae survived. When frozen in scats the rate of emergence was significantly lowered.

The larvae were able to make directed movements in gelatine but not in water. They showed positive chemosensitivity to snail mucus.

Measurements in the field of temperatures and humidities indicated that autumn and spring are the most favourable seasons for larvae survival.

New invasions of Mustela spp. by S.nasicola were found in the cold months of the year. The mean numbers of S.nasicola per host individual were higher in winter-spring than in autumn. The mean length of S.nasicola was highest in autumn, being significantly lower in spring when the frequency distributions were binodal.

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Fig. 1. Rate of emergence of larvae of Skrjabingylus nasicola from wet scats at room temperature (+22°C). Separate and mean mean values shown.

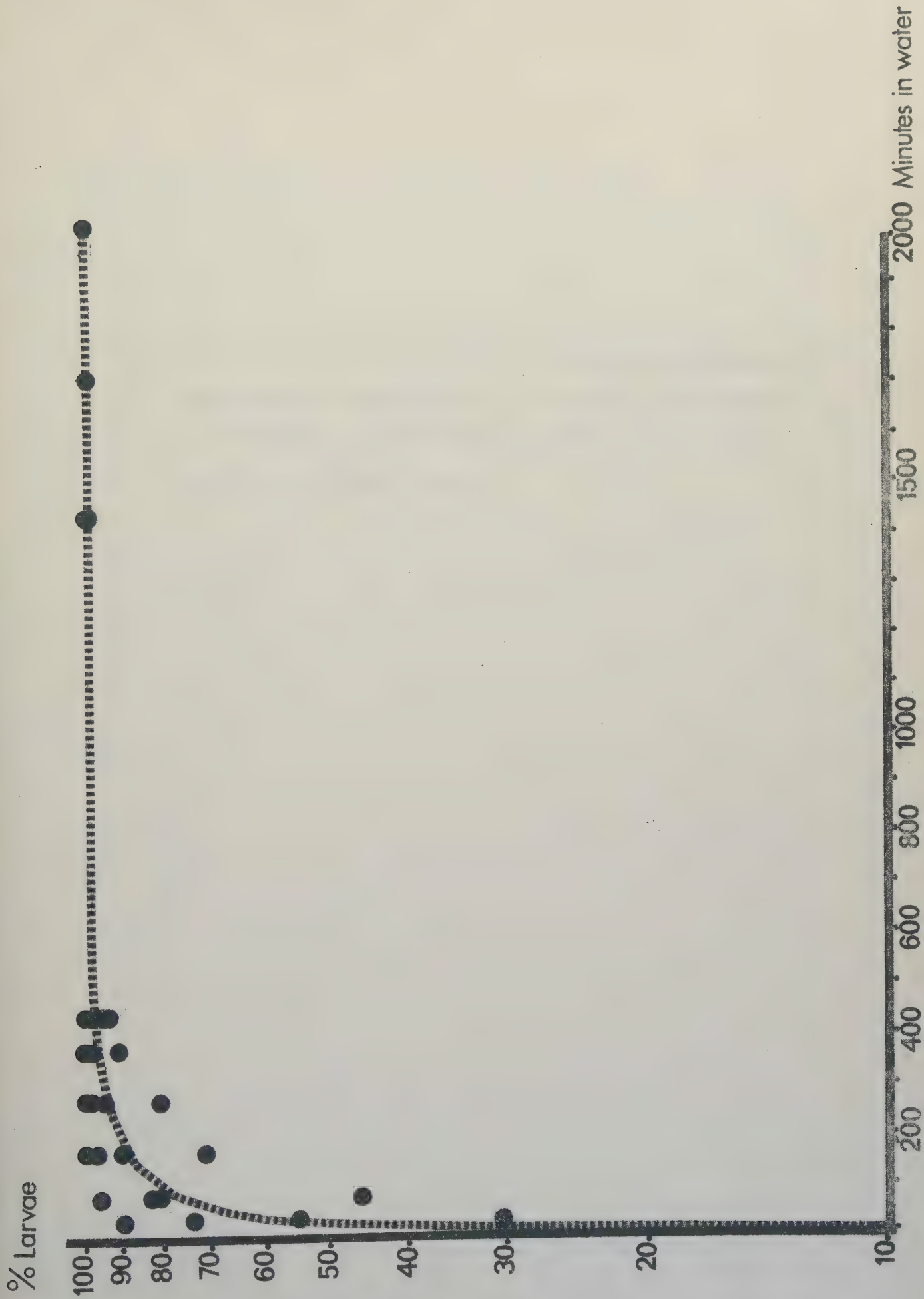




Fig. 2. Rate of emergence of larvae of Skrjabingylus nasicola from wet scats at temperatures of $\pm 0^{\circ}\text{C}$ (~~~~), $+4^{\circ}\text{C}$ (|||||), $+15^{\circ}\text{C}$ (————) and $+26^{\circ}\text{C}$ (■■■■). Mean values and $\pm$ one standard deviation shown.

% Larvae

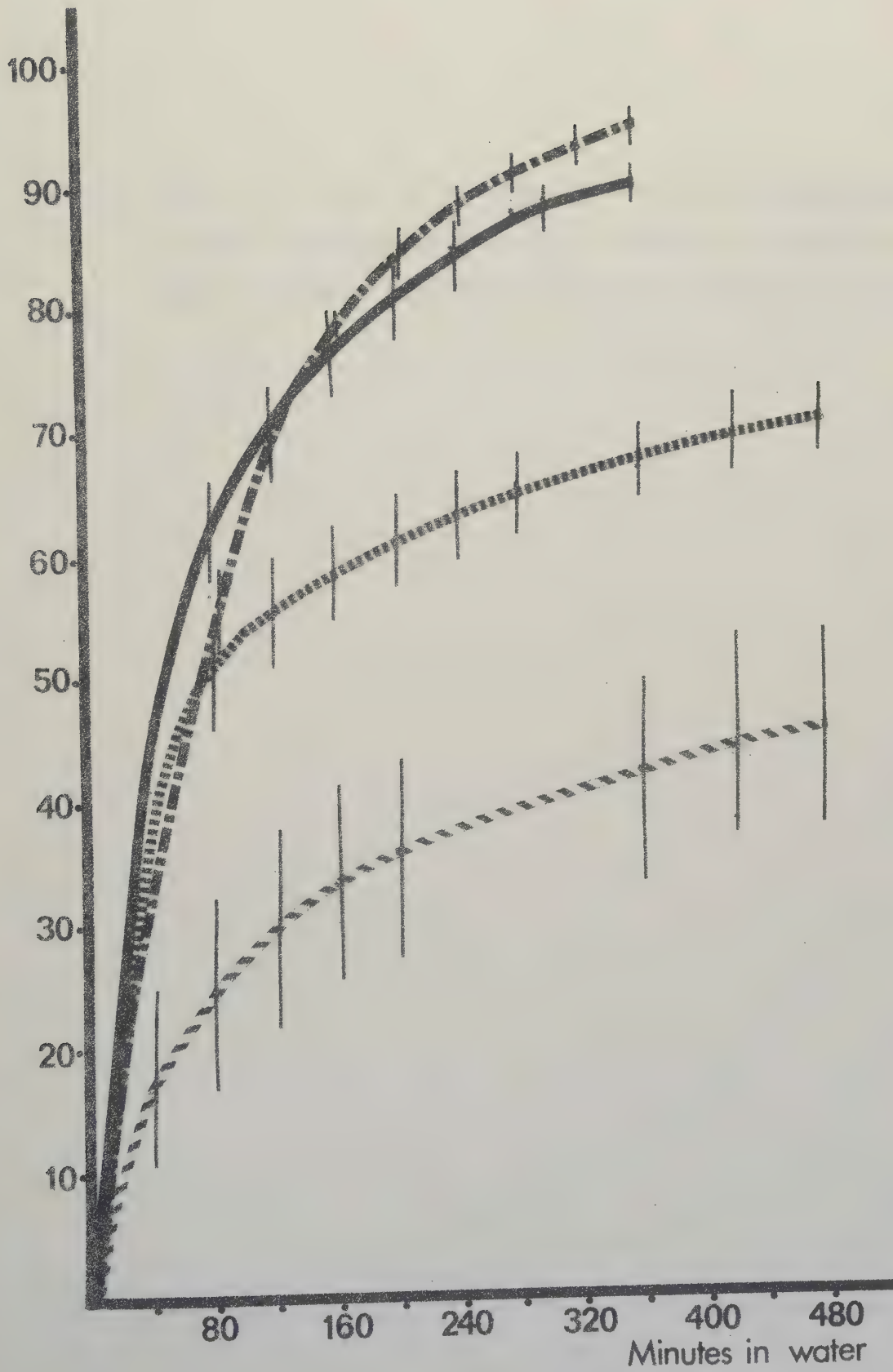


Fig. 3. Duration in days of ability of larvae of Skrjabinogylus nasicola to swim within 30 minutes of the addition of water to scats kept at different relative humidities and temperatures.

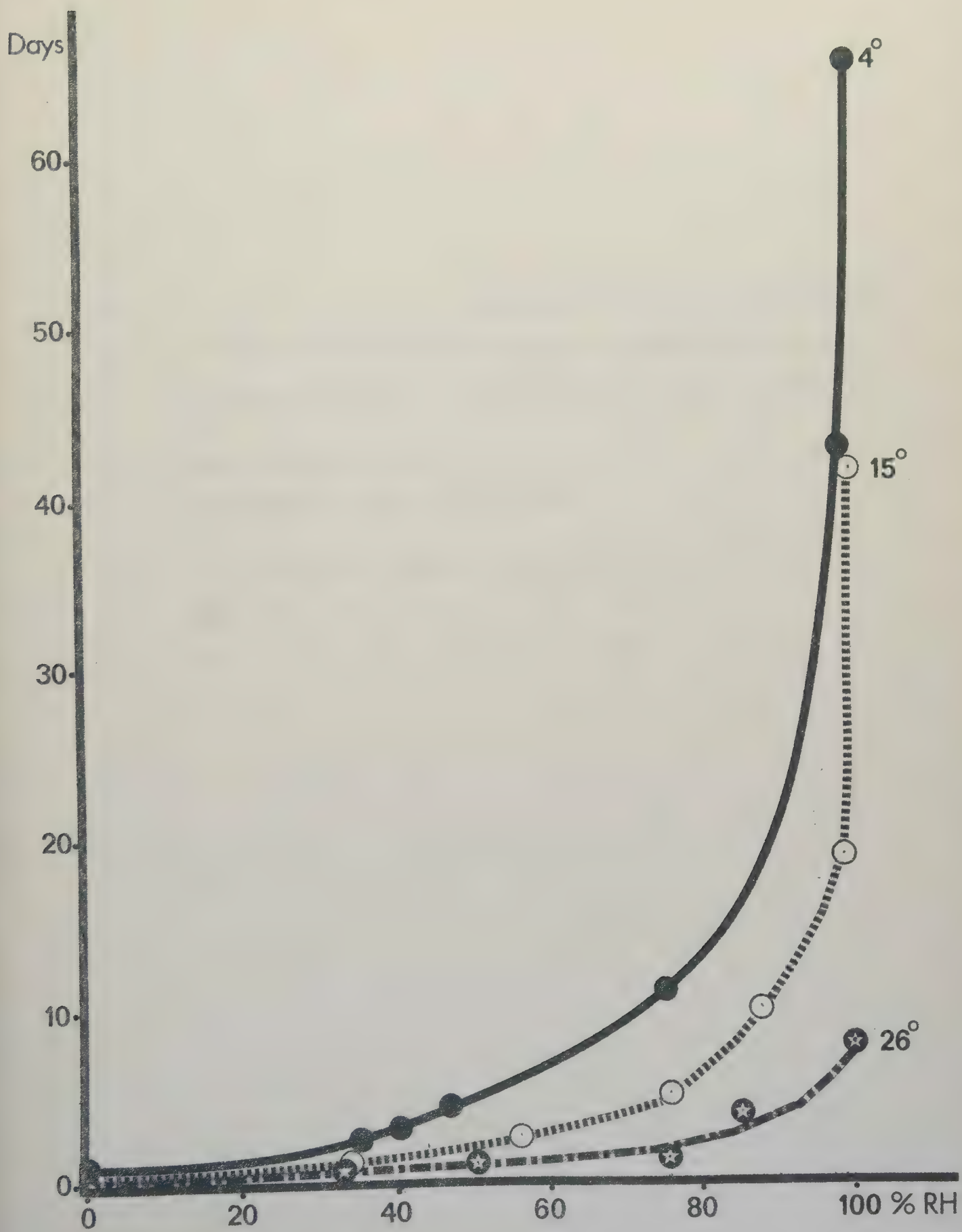


Fig. 4. The effect on larvae of Skriabingylus nasicola of desiccation at +24°C and 40% relative humidity expressed as percentage of active larvae found at intervals after water was restored.

—— Swimming larvae

||||| Swimming + less active larvae

○	Larvae desiccated for 2 minutes (43 specimens)
●	" " " 3 " (31 ")
☆	" " " 5 " (49 ")

% Larvae

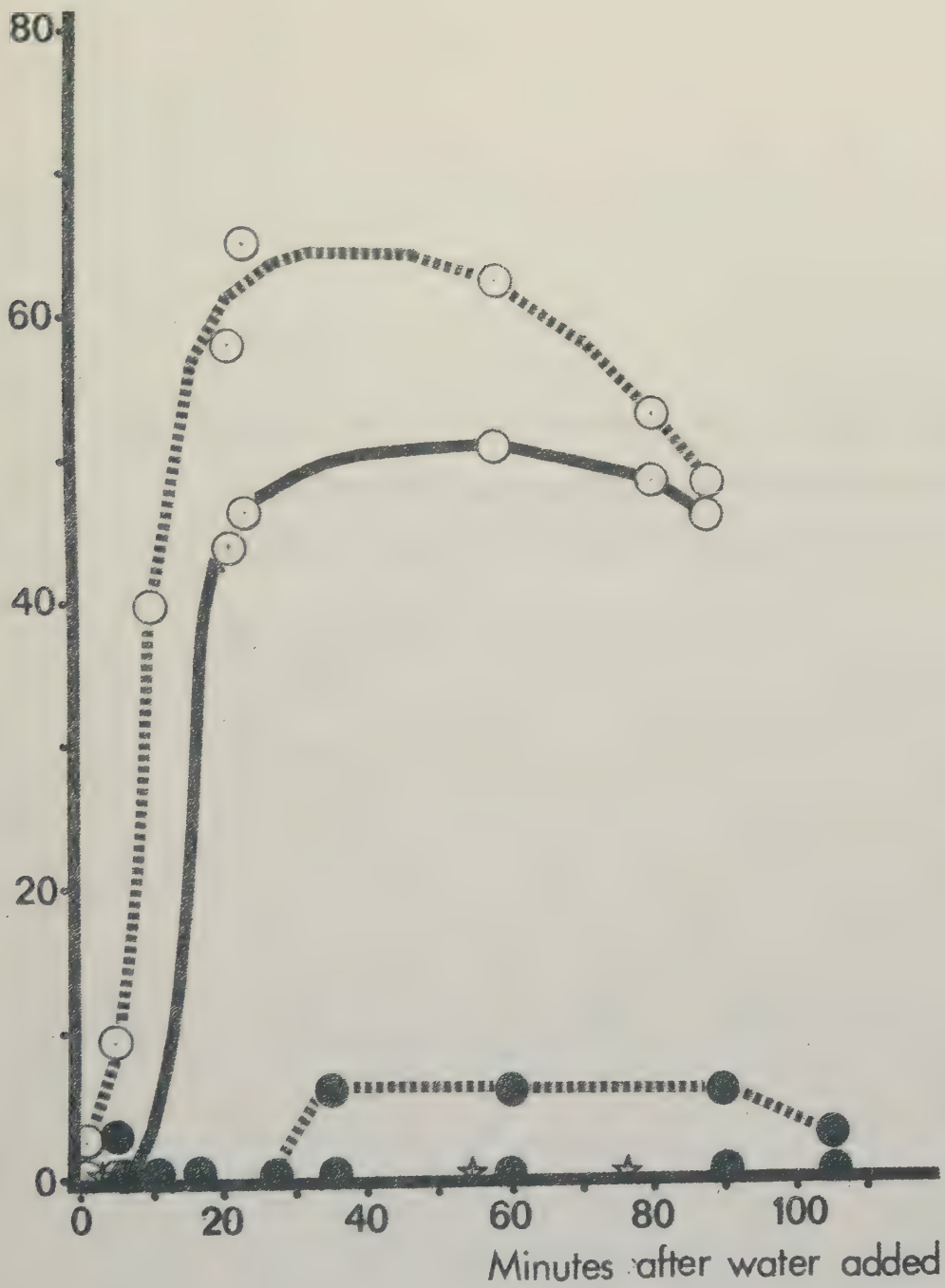




Fig. 5. Rate of decrease in swimming activity of not agitated larvae of Skriabingylus nasicola in aerated water. Percentage of swimming larvae shown (100% swimming larvae at start).

●	92	larvae	in	the	series
○	158	"	"	"	"
☆	224	"	"	"	"
★	55	"	"	"	"

% Larvae

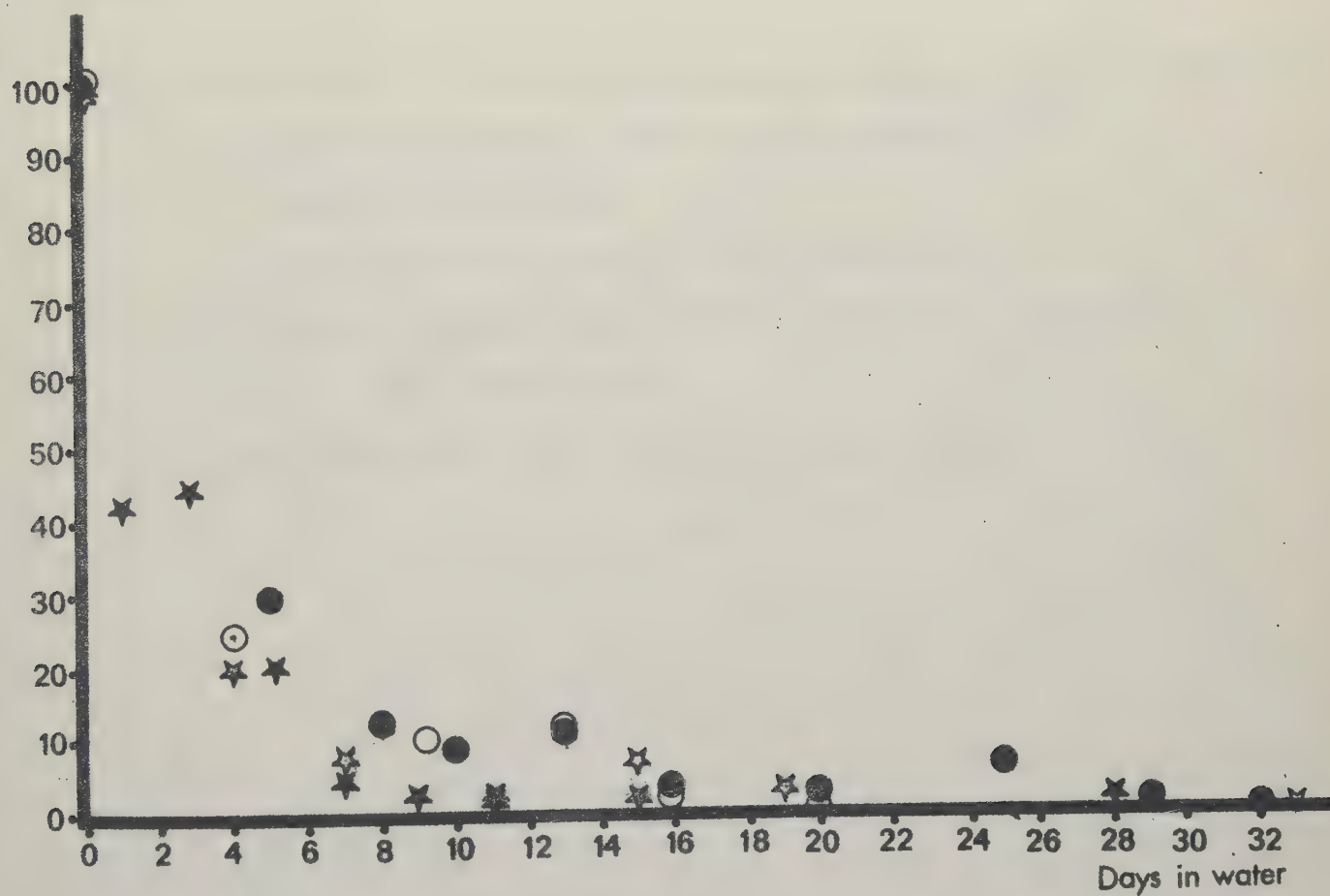


Fig. 6. The effect of freezing Skrjabingylus nasicola larvae in scats, expressed as emergence rates from wet scats at +15°C.

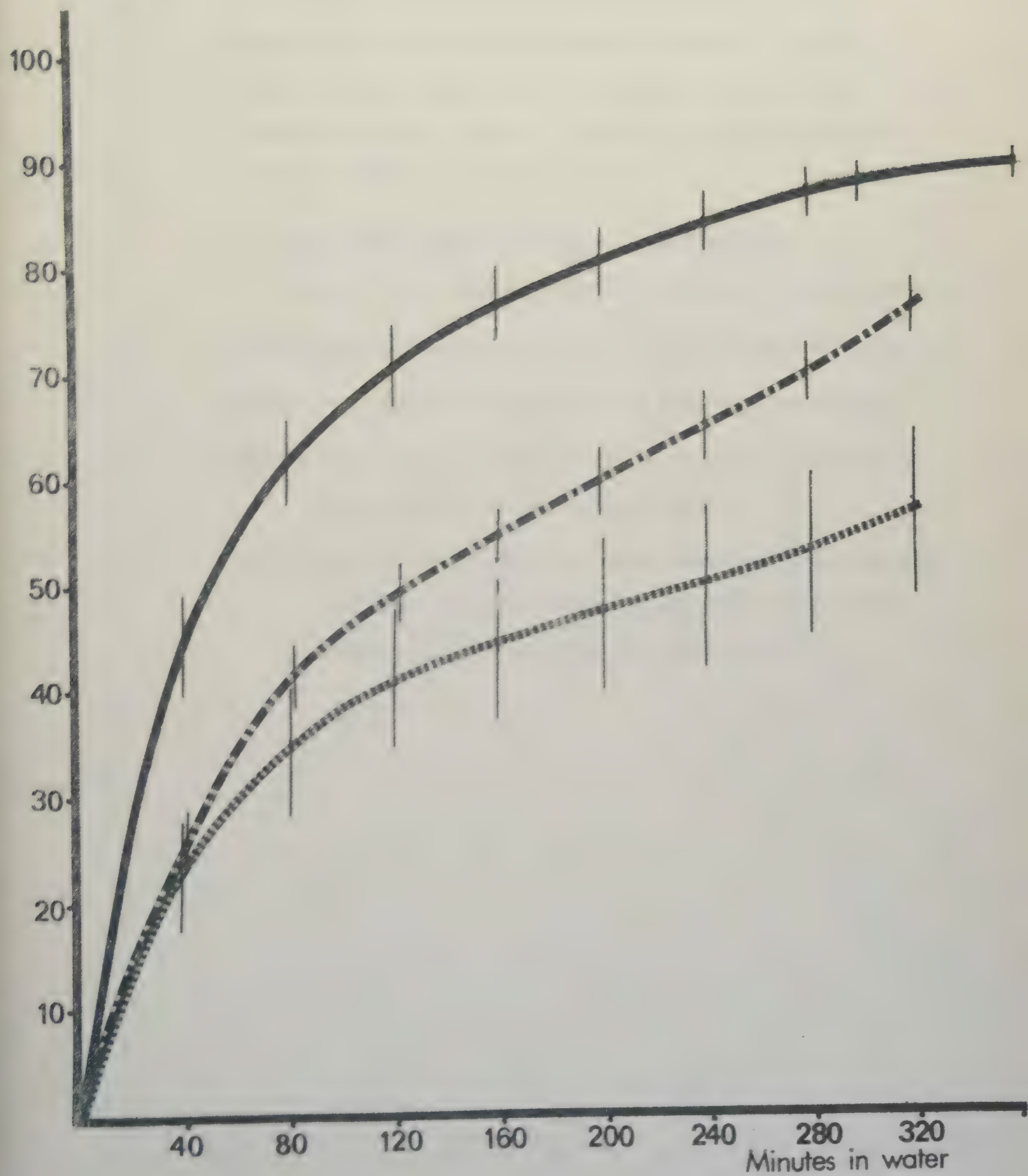
(1)  from fresh scats

(2)  from scats frozen at -5°C (4x24 hours)

(3)  from scats frozen at -5°C (4x24 hours) and thawed at +4°C (4x24 hours)

Mean values and $\pm$ one standard deviation shown.

% Larvae



Figs. 7-8. Seasonal changes in mean maximum, mean minimum and overall mean temperatures and relative air humidities at scat deposition sites of mink in central Scania. - Fig. 7. Temperature and humidity of a sheltered log in swampy brushwood (birch). - Fig. 8. Temperature and humidity at a wooden bridge in an open meadow.

I: spring (March-May); II: summer (June-August);

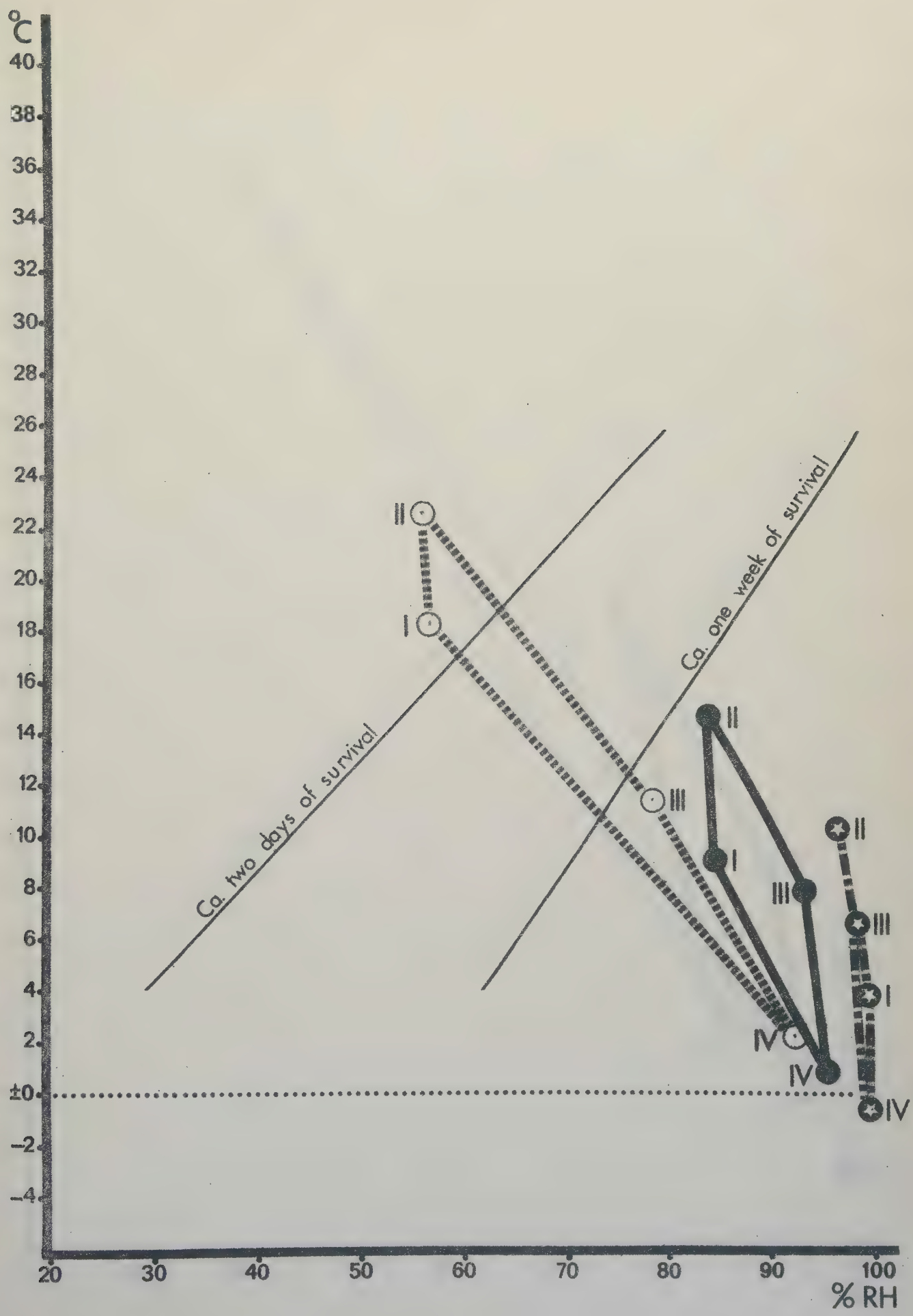
III: autumn (September-November); IV: winter (December-February).

○■■■■ Mean maximum temperature and mean minimum humidity.

★■■■■ Mean minimum temperature and mean maximum humidity.

●■■■■ Mean values of temperature and humidity (calculated from the data of every second hour).

—— Lines joining points of equal survival of S. nasicola larvae in mustelid scats (M. putorius) at constant temperature and humidity according to Fig. 3.



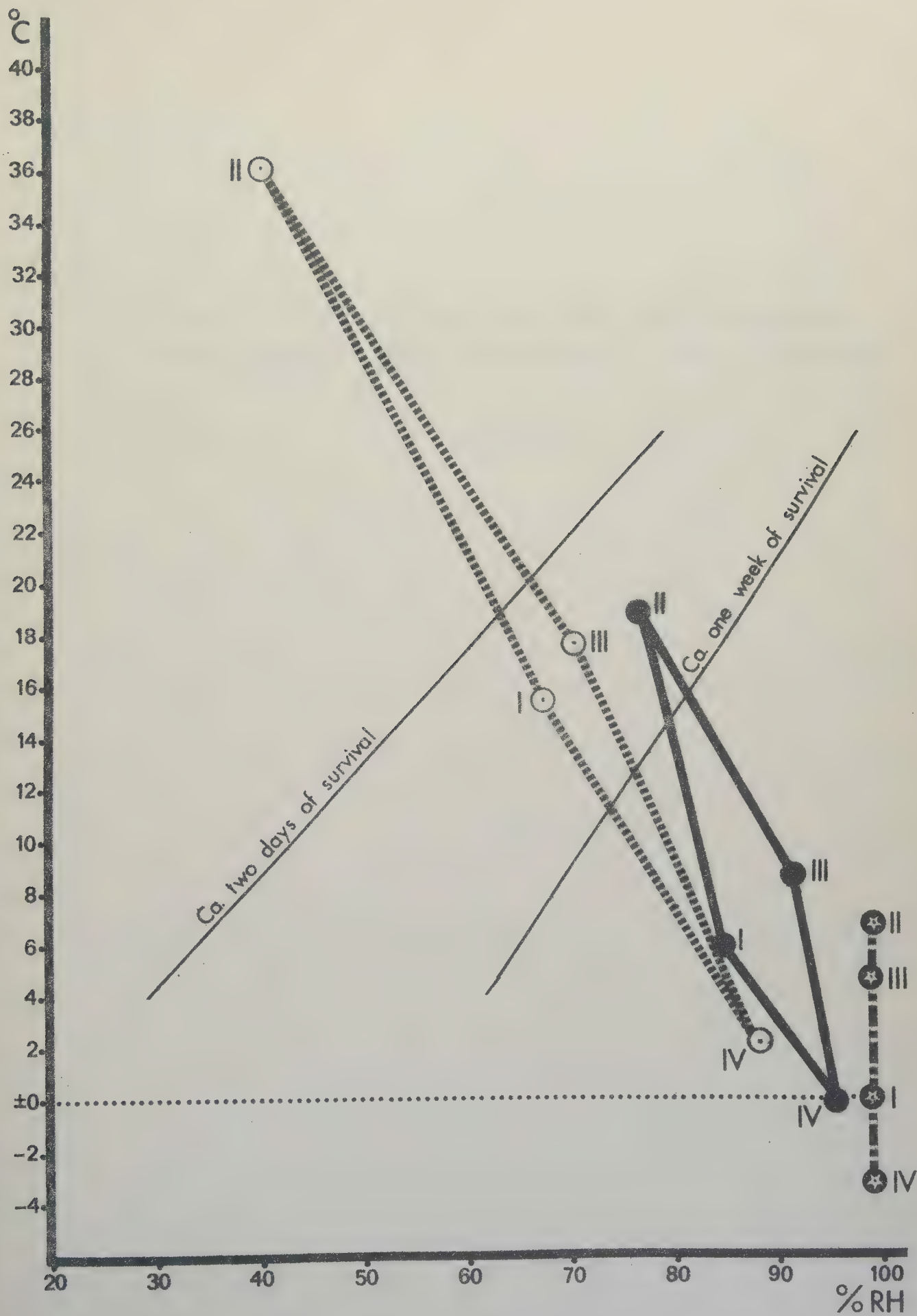


Fig. 9. Seasonal variation in body length distribution of S. nasicola
from M. erminea, northern Sweden (region III+IV in Hansson 1970).

Number of
S. nasicola

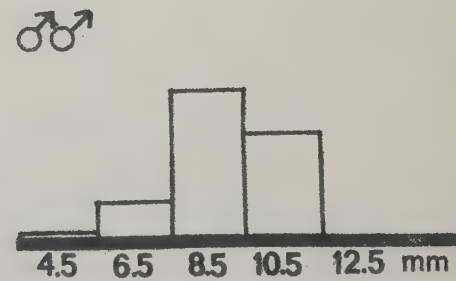
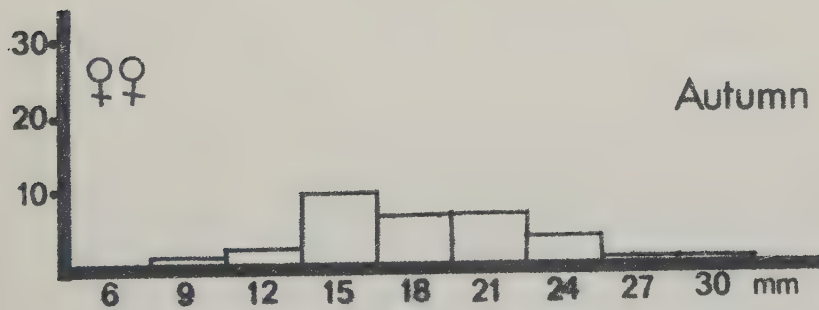
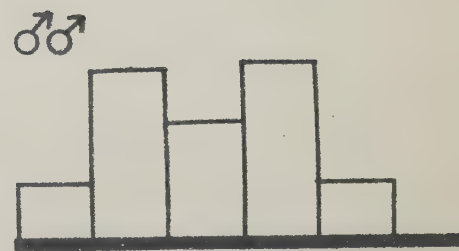
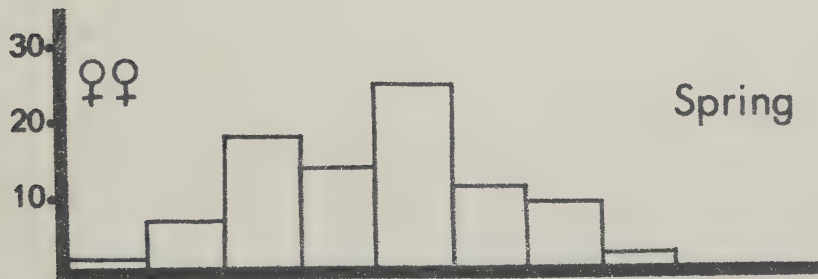
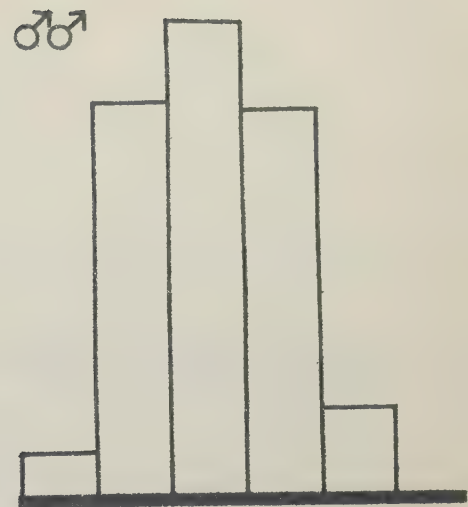
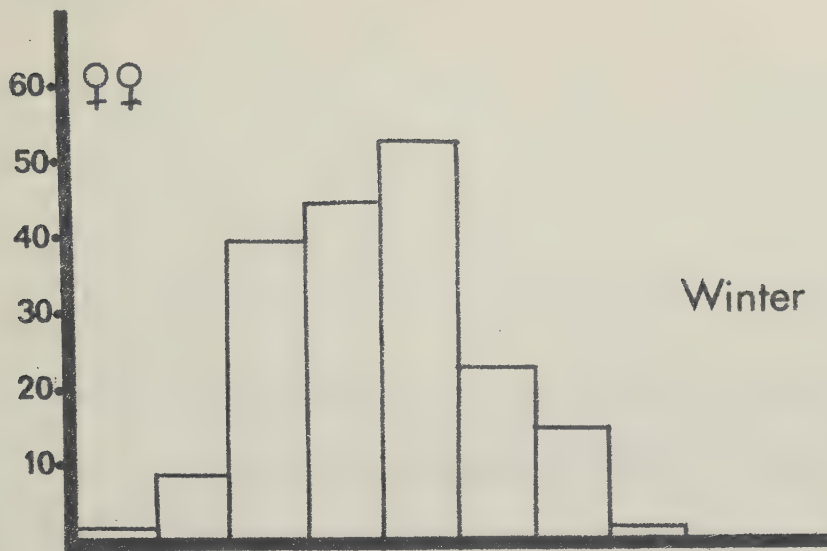


Fig. 10. Seasonal variation in body length distribution of S. nasicola
from M. putorius, Southern Sweden.

Number of
S. nasicola

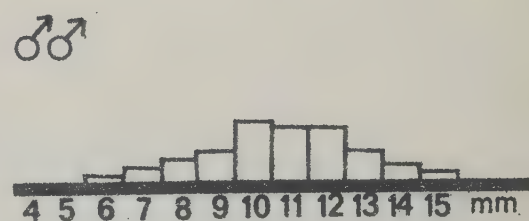
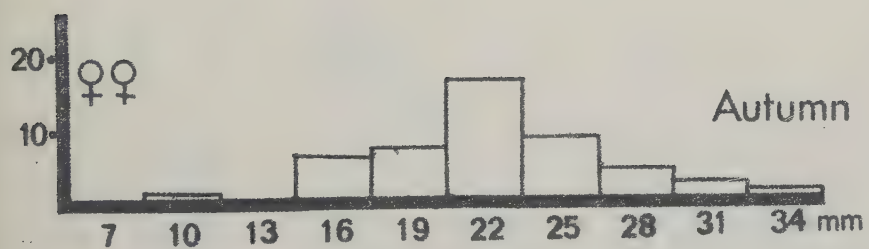
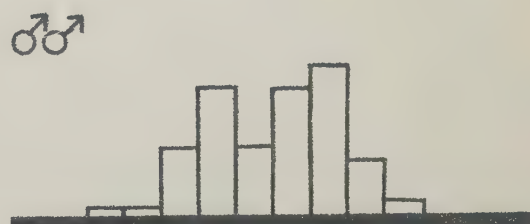


Table 1. Frequency and size of S. nasicola in different population categories of Mustela spp. invaded for four weeks or less. Age groups are as in Hansson 1968 (suturæ nasales: coalescing-age group 2 coalesced, visible-3, invisible-4).

<u>Mustela</u> spp.	Sex	Trapping data	Number of <u>S. nasicola</u>		Ranges of nematode lengths in mm.		Notes of invasion	Age group	
			♂♂	♀♀	without free larvae	♂♂	♀♀		
<u>M. nivalis</u>	♂	Västergötland 28.11.1962	3	3	1	6.0-8.0	7.0-10.5	Probably one early simultaneous invasion	2
<u>M. erminea</u>	♂	Jämtland 8.1.1962	5	10	2	4.0-8.0	6.0-21.0	Reinvasion	3
"	♂	Norrbotten 7.2.1965	15	13	1	7.0-12.5	8.0-25.5	Reinvasion	3
"	♂	Jämtland 12.2.1962	9	19	2	6.8-10.5	7.8-22.2	Reinvasion	-
"	♂	Lappland 15.25.2.1967	2	2	1	7.0, 7.5	10.5, 120	Probably one early simultaneous invasion	3
"	♀	Lappland 17.2.1962	21	21	1	6.3-12.0	13.5-24.0	Reinvasion	4
"	-	Jämtland 20.3.1962	24	23	7	5.0-10.0	5.0-17.0	Reinvasion	4
"	♂	Ångermanland 20.3.1962	12	7	2	5.0-12.0	11.5-23.5	Reinvasion	4
"	♂	Västerbotten Dec. 1961	13	18	3	6.0-12.2	9.5-21.3	Reinvasion	4
<u>M. vison</u>	♂	Värmland 16.10.1965	1	1	1	5.5	8.0	First invasion	2
<u>M. putorius</u>	♂	Skåne 17.5.1967	13	15	1	8.0-14.0	8.0-24.0	Reinvasion	4
"	♂	Skåne 29.12.1961	9	9	1	4.5-12.0	6.0-21.0	Reinvasion	3

